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ANATOMICAL AND FUNCTIONAL DATA ON FEMALE AND MALE REPRODUCTIVE SYSTEMS OF SOME DUNG BEETLE SPECIES OF APHODIINAE AND EUPARIINAE OF MEXICO (COLEOPTERA: SCARABAEOIDEA: APHODIIDAE)

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Abstract.—Female and male reproductive systems of two species of Aphodiinae, *Aphodius opisthius* and *Cephalocyclus hogei,* as well as of one species of Eupriinae, *Ataenius apicalis* are described. Comparisons are then made between 11 species of both subfamilies. The reproductive systems of both sexes of Aphodiinae and Eupariinae are similar, but there are differences between species of the two Aphodiinae genera and between the two subfamilies. In females, ovarioles number in each ovary varies among species. The genital chamber of *Aphodius* and *Ataenius* is similar, but seems different in *Cephalocyclus.* The spermathecae are variable according to species. The spermathecal duct and spermathecal glandular duct originates in the same place in *Aphodius,* but not in *Ataenius* and *Cephalocyclus.* Males of *Aphodius* have 7, *Cephalocyclus* have 6, and *Ataenius* have 2 testicular follicles. The seminal vesicle only is present in *Cephalocyclus.* The glandular reservoirs are similar in *Aphodius* and *Cephalocyclus,* but differentet in *Ataenius.* The anterior part of ejaculatory duct and the internal sac differ among species of the two subfamilies. The preputial ventral gland only is present in *Aphodius* and *Cephalocyclus.*

Resumen.—Se describe el aparato reproductor de hembras y machos de dos especies de Aphodiinae, *Aphodius opisthius* y *Cephalocyclus hogei,* y de una especie de Eupriinae, *Ataenius apicalis,* y se hacen las comparaciones entre las 11 especies examinadas de las dos subfamilias. El aparato reproductor de las hembras y los machos de Aphodiinae y Eupariinae están conformados anatómicamente de manera semejante. Sin embargo, existen diferencias entre las especies de los dos géneros de Aphodiinae y de las dos subfamilias. En las hembras el número de ovariolas por ovario es variable según la especie. La cámara genital es semejante en *Aphodius* y *Ataenius,* en *Cephalocyclus* es diferente. Las espermatecas son diferentes de especie a especie. El conducto espermatecal y el conducto de la glándula de la espermateca se originan en el mismo sitio en *Aphodius*; no así en *Ataenius* y en *Cephalocyclus.* En los machos de *Aphodius* hay 7 folículos testiculares, *Cephalocyclus* tiene 6 y *Ataenius* tiene 2. La vesícula seminal sólo existe en *Cephalocyclus.* Los reservorios glandulares son semejantes en *Aphodius* y *Cephalocyclus,* en *Ataenius* son diferentes. La parte anterior del conducto eyaculador y el saco interno difieren entre las especies de las dos subfamilias. La glándula prepucial ventral sólo se presenta en *Aphodius* y *Cephalocyclus.*

Key Words: *Aphodius, Cephalocyclus, Ataenius,* females, males, anatomy, spermatophore

The family Aphodiidae (Scarabaeoidea) (sensu Balthasar 1963) is composed of 8 tribes and 29 genera, containing 3,400 species worldwide. The subfamily Aphodiinae consists of about 1,750 species, of which 94% belong to the genus *Aphodius* (Dellacasa 1987). The species of this genus are commonly refered to as aphodiine dung beetles. Because the focus of this paper is morphology, we have chosen to use the traditional taxonomic classification, although the subgenera of *Aphodius* have been raised to the rank of genus by Dellacasa et al. (2000). The subfamily Eupariinae contains 593 species, of which 54% belong to the genus *Ataenius* which contains about 228 American species (Deloya 1994). Aphodiidae species are characteristic of temperate regions in the Northern Hemisphere, although some important species are found in subtropical and tropical regions (Hanski and Cambefort 1991).

The reproductive system of Aphodiidae has not been well studied. Knowledge of the female anatomy consists solely of some very generalized schemes (Willimzik 1930, Lumaret 1980, Yoshida 1994). The number of ovarioles per ovary is known for only 29 species of Aphodiinae, 2 of Eupariinae, and 3 of Psammodiinae (Stein 1847, Willimzik 1930, Ritcher and Baker 1974, Yasuda 1987, Yosida 1994, Gittings and Giller 1997).

The male reproductive system has been described for only 15 species of Aphodiinae and 2 of Eupariinae (Bordas 1900, Pluot-Sigwalt and Martínez 1998). The histological structure of the testes is known for 9 species of *Aphodius* and 2 of *Ataenius,* and of spermatozoa for 2 species of *Aphodius* and 4 of *Ataenius* (Virkki 1957, Martínez and Cruz 1999). Spermatogenesis has been studied in 10 *Aphodius* species (Virkki 1951).

The paucity of literature on reproductive system anatomy in Aphodiidae species, and the need to characterize it in order to understand their reproductive cycles, motivated for this morphological study.

Materials and Methods

Most of the species examined were collected in dung pats in various pastures, largely in the state of Veracruz, Mexico: Aphodiinae: *Aphodius* (*Trichaphodius*) *opisthius* Bates, from Cuiyachapa, Veracruz; *A.* (*Planolinus*) *vittatus* Say, from Las Vigas, Veracruz; *A.* (*Bodillus*) *sallei* Harold, from La Mancha, Veracruz; *A.* (*Labarrus*) *pseudolividus* Balthasar, from Alto Lucero, Veracruz; *A.* (*Nialaphodius*) *nigrita* Fabricius, from Quiahuistlán, Veracruz; *Cephalocyclus hogei* Bates, from Cuiyachapa, Veracruz. Eupariinae: *Ataenius apicalis* (Hinton) and *At. sculptor* Harold, from Los Lirios, Actopan, Veracruz; *At. cribrithorax* Bates, from Los Tuxtlas, Veracruz; *At. paraperforatus* Deloya and Ibañez-Bernal (2000), from Ohuapan, Veracruz; and *At. setiger* Bates, from Tuxpan, Iguala, Guerrero (caught in a light trap at night).

For each species, 5 to 30 individuals of each sex were examined. The reproductive system was dissected in Ringer solution. Subsequently, the material was fixed in AFATD (96% ethanol-formaldehyde-trichloroacetic acid-dimethylsulfoxide), in which it was extended, and then stored in 96% ethanol. In some cases, the reproductive system was completely stained, using the Feulgen-green light technique and mounted whole in Canada balsam (Gabe 1968, Martínez 1999). To observe cuticular structures, the reproductive system was stained with chlorazol black after maceration with 5% potassium hydroxide (Carayon 1969). During dissection and after fixation and staining, the reproductive system was drawn to scale with the help of a camera lucida. In the present study, we follow the anatomical terminology of Snodgrass (1935) and Matzuda (1976).

Results

Females

The reproductive system of *Aphodius, Cephalocyclus,* and *Ataenius* females consists of two ovaries, two lateral oviducts, one common oviduct, a genital chamber, and the spermatheca along with its gland.

Aphodius opisthius (Fig. 1A).—Each ovary is generally formed of 9 telotrophic ovarioles, although sometimes there are only 8. Each ovariole has a terminal filament, germarium, vitellarium, and pedicel. The ovarioles for each ovary are covered in a fine membrane, the peritoneal sheath, which at its apex forms the ovary's long terminal filament. The vitellarium has oocytes of two notably different sizes. The pedicels of each ovary lead into the respective lateral oviduct. Basal oocytes of any ovariole mature simultaneously.

The lateral oviducts lead into the common oviduct, which is slightly longer than the lateral oviducts. The exterior walls of all oviducts are formed of circular muscles. The common oviduct narrows before joining the anterior part of the genital chamber.

Dissection reveals the genital chamber to be a relatively bulky organ surrounded by numerous, strong muscles that run circularly and longitudinally. After treatment with the potassium hydroxide solution and staining, this organ is found to consist of two quite different regions: an anterior part that corresponds to the bursa copulatrix, and a posterior part that might be considered as some type of vaginal sac (Fig. 2A). The bursa copulatrix is wider where the common oviduct joins it; it narrows until it meets the vulva, at about the same height as the vaginal sac. The spermathecal duct ends medio-ventrally, very close to the end of the oviduct. The vaginal sac, ventral to the bursa copulatrix, is wide and rounded, and shorter that the bursa copulatrix; it narrows until it terminates in the vulva or gonopore. The vulva and the anus, ventral to the vulva, end in a common space that might be thought of as a cloaca.

The bursa copulatrix has a thick cuticular intima with many longitudinal folds. The folds are especially numerous in the area where the common oviduct and spermathecal duct terminate. The vaginal sac has a very thick cuticular intima, with little folding, and lateral, circular, highly sclerotized structures that have spines throughout their expanse (Fig. 2A).

The spermatheca or spermathecal capsule is also sclerotized, C-shaped, with a broad, relatively flat base and a narrow apex, which is more rounded and less sclerotized than the base. Muscles are found between the apex and the base. The spermathecal duct issues from the base of the spermatheca, is thin and up to 4 to 5 mm long, and curls around itself before joining the bursa copulatrix. Dissection reveals the spermathecal gland to be voluminous, almost spherical, and with a rough wall formed by the epidermal glands (Fig. 1A). After treating the spermatheca with potassium hydroxide, the glandular reservoir appears long, with a very thin, cuticular wall and a short duct that joins the base of the spermatheca beside the beginning of the spermathecal duct (Fig. 3).

Comparison of *Aphodius* females.—The number of ovarioles per ovary varies, 8 or 9 in *A. opisthius,* but only 5 in *A. vittatus, A. sallei, A. pseudolividus,* and *A. nigrita.* All *Aphodius* species have 2 oocytes in the vitellarium, except for *A. pseudolividus,* which has 3. The size of the mature basal oocyte, with chorion, varies with the species (Table 1). Basal oocyte maturation is simultaneous in all ovarioles in individuals of all species examined.

The genital chamber is formed by the bursa copulatrix and vaginal sac in all *Aphodius* species. The anterior part of the genital chamber, where the common oviduct joins, is highly folded and relatively

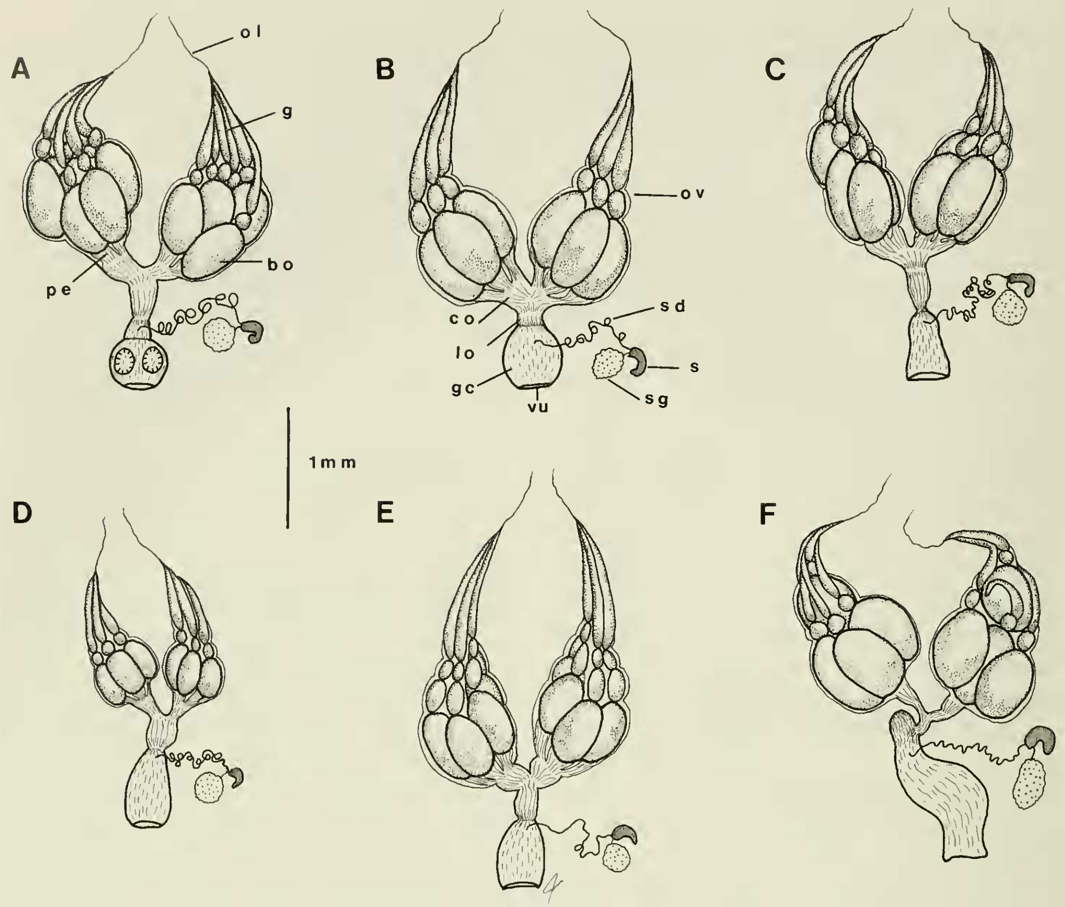

Fig. 1. Reproductive system schemes in Aphodiinae females. A, *Aphodius opisthius.* B, *A. sallei.* C, *A. vittatus.* D, *A. nigrita.* E, *A. pseudolividus.* F, *Cephalocyclus hogei.* (Abbreviations: bo = basal oocyte; co = common oviduct; sd = spermathecal duct; g = germarium; gc = genital chamber; lo = lateral oviduct; ol = ovarial ligament; ov = ovary; pe = pedicel; s = spermatheca; sg = spermathecal gland; vu = vulva or gonopore).

enlarged in *A. opisthius* and *A. sallei,* and less folded and enlarged in *A. vittatus, A. nigrita,* and *A. pseudolividus* (Figs. 2A–E). In most *Aphodius* species, the bursa copulatrix and vaginal sac are separated, and emerge nearly independently very close to the vulva (Figs. 2A–D), except in *A. pseudolividus,* in which the bursa copulatrix and vaginal sac are not entirely separate and join much before reaching the vulva (Fig. 2E). In the bursa copulatrix, the spermathecal duct emerges very close to the opening of the common oviduct in all species except *A. pseudolividus,* in which the spermathecal duct emerges farther from the common oviduct (Fig. 2E). The cuticular intima in this region varies depending on species; the termination of the spermathecal duct is found only among the folds of the anterior region, as in *A. opisthius* and *A. sallei* (Figs. 2A, B) or at the back of a folded structure having a funnel-like form, as in *A. vittatus, A. nigrita,* and *A. pseudolividus* (Figs. 2C–E).

The vaginal sac is shorter than the bursa copulatrix in all *Aphodius* species, but its structure varies among the species. The cuticular intima is smooth and thick in *A. opisthius, A. sallei,* and *A. nigrita* (Figs. 2A, B, D), slightly folded in *A. pseudolividus* (Fig. 2E), and very folded in *A. vittatus*

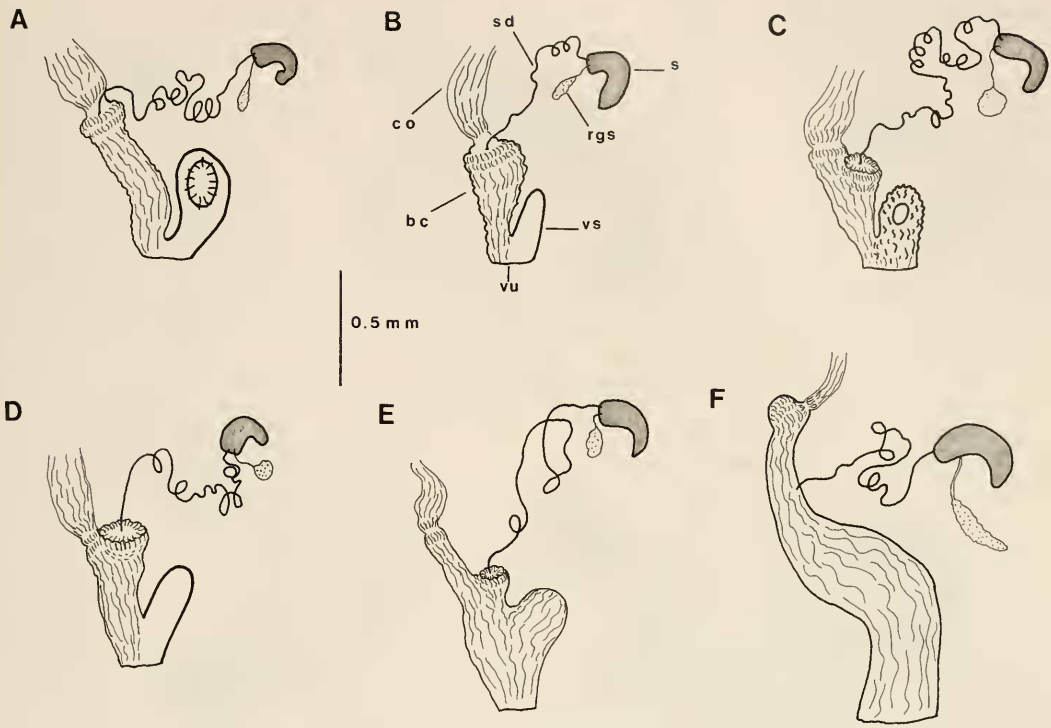

Fig. 2. Female Aphodiinae genital chambers after treatment with potassium hydroxide and chlorazol black. A, *Aphodius opisthius.* B, *A. sallei.* C, *A. vittatus.* D, *A. nigrita.* E, *A. pseudolividus.* F, *Cephalocyclus hogei.* (Abbreviations: bc = bursa copulatrix; co = common oviduct; rgs = reservoir of spermatheca gland; s = spermatheca; sd = spermathecal duct; vs = vaginal sac; vu = vulva or gonopore).

Table 1. Anatomical data on the female reproductive system of Aphodiinae and Eupariinae (n, number of the females per species examined in the present study).

Species	Individuals (n)	Cephalo-caudal Length (mm)	Ovarioles per Ovary (number)	Mature in Vitellarium Oocytes (number)	(mm)
APHODIINAE					
Aphodius opisthius	30	4.5	9–9*	2	0.90
A. vittatus	20	4.0	5–5	2	0.85
A. sallei	20	5.0	5–5	2	0.80
A. nigrita	6	3.5	5–5	2	0.50
A. pseudolividus	25	5.0	5–5	3	0.65
Cephalocyclus hogei	30	6.0	5–5	2	0.90
EUPARIINAE					
Ataenius apicalis	30	6.0	8–8*	2	0.75
At. sculptor	30	6.0	9–9	3	0.80
At. cribrithorax	20	4.0	3–3	4	0.60
At. setiger	10	4.5	3–3*	3	0.55
At. paraperforatus	10	6.0	11–11	3	0.50

* Number of ovarioles per ovary varies within and among females of the same species.

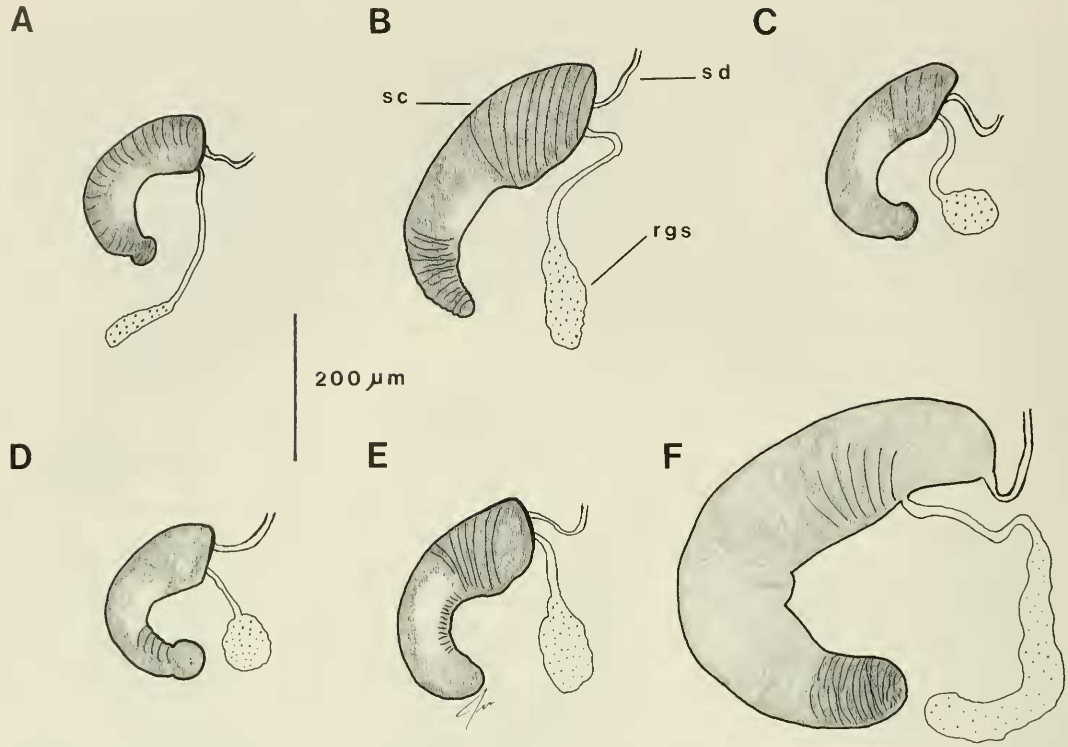

Fig. 3. Spermatheca schemes in Aphodiinae females. A, *Aphodius opisthius*. B, *A. sallei*. C, *A. vittatus*. D, *A. nigrita*. E, *A. pseudolividus*. F, *Cephalocyclus hogei*. (Abbreviations: sd = spermathecal duct; rgs = reservoir of spermatheca gland; sc = spermathecal capsule).

(Fig. 2C). Further, some species show cuticular areas that are very sclerotized, [as in *A. opisthius* (Fig. 2A)], less sclerotized, [as in *A. vittatus* (Fig. 2C)], or not sclerotized at all [as in *A. sallei, A. nigrita,* and *A. pseudolividus* (Figs. 2B, D, E)].

The form of the spermatheca and the cuticular reservoir of the spermathecal gland differs from species to species, but the spermathecal duct is long in all species (Figs. 2, 3). In all *Aphodius* species, the spermatheca is curved, with a flat and sclerotized base. The apex may be rounded, as in *A. opisthius,* more spherical, as in *A. sallei, A. vittatus,* and *A. nigrita,* or relatively pointed, as in *A. pseudolividus.* The spermathecal gland reservoir joins the base of the spermatheca beside the spermathecal duct in all species. However, its form varies, being long in *A. opisthius* and *A. sallei,* almost spherical in *A. vittatus* and *A. nigrita,* and rounded in *A. pseudolividus* (Fig. 3).

Cephalocyclus hogei (Fig. 1F).—The reproductive system anatomy is similar to those of *Aphodius* species, but their genital chamber is different. Each ovary has 5 ovarioles. Each ovariole contains 2 oocytes, which are of two notably different sizes. Basal oocytes mature simultaneously in all oviaroles. Each ovary has a lateral oviduct attached, and these 2 oviducts join the short common oviduct. A distinctive character of this species is that the genital chamber is a sac-like vagina, very elongated, with thick walls, enlarged and with numerous folds in its anterior region; the genital chamber then narrows markedly when it approaches and terminates in the vulva. There is no separation between the bursa copulatrix and the vaginal sac. The common oviduct joins the

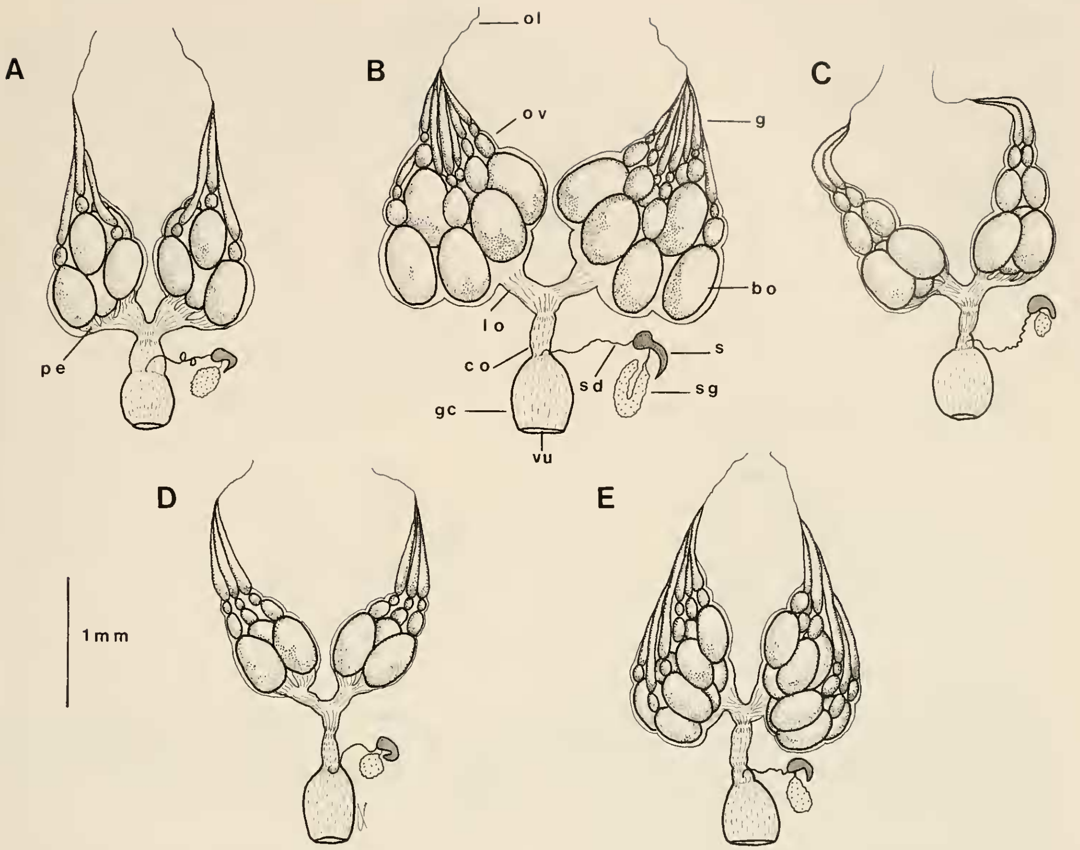

Fig. 4. Reproductive system schemes in Eupariinae females. A, *Ataenius apicalis*. B, *At. sculptor*. C, *At. cribrithorax*. D, *At. setiger*. E, *At. paraperforatus*. (Abbreviations: bo = basal oocyte; co = common oviduct; sd = spermathecal duct; g = germarium; gc = genital chamber; lo = lateral oviduct; ol = ovarial ligament; ov = ovary; pe = pedicel; s = spermatheca; sg = spermathecal gland; vu = vulva or gonopore).

chamber laterally, beneath the anterior swelling of the vagina. The spermathecal duct joins the medio-ventral region where the vagina narrows, somewhat distant from the entry of the common oviduct. The cuticular intima of the genital chamber is thick and shows numerous longitudinal folds, more numerous folds than those of the anterior swelling (Fig. 2F).

The spermatheca is curved, with a rounded base which is slightly wider than the apex. From the basal region, the long spermathecal duct, measuring up to 4 mm, emerges and then curls for its entire trajectory until it joins the medio-ventral region of the vagina. The spermathecal gland is oval with a rugged surface. After treatment with potassium hydroxide, the cuticular reservoir is seen to be fusiform and pointed (Fig. 2F), and its duct joins the medio-ventral region of the base of the spermatheca (Fig. 3F).

Ataenius apicalis (Fig. 4A).—The ovaries have a variable number of ovarioles, most (n = 20) have 8 ovarioles per ovary, while a minority (n = 7) have 7 or 8 in the same female and a few (n = 3) have 8 or 9. The ovarioles in each ovary are wrapped in a peritoneal sheath that ends in the ovarial ligament. Each ovariarole is telotrophic, having a terminal filament, germarium, vitellarium, and pedicel. In mature females, each vitellarium has two oocytes. Pedicels join their respective lateral oviducts, which

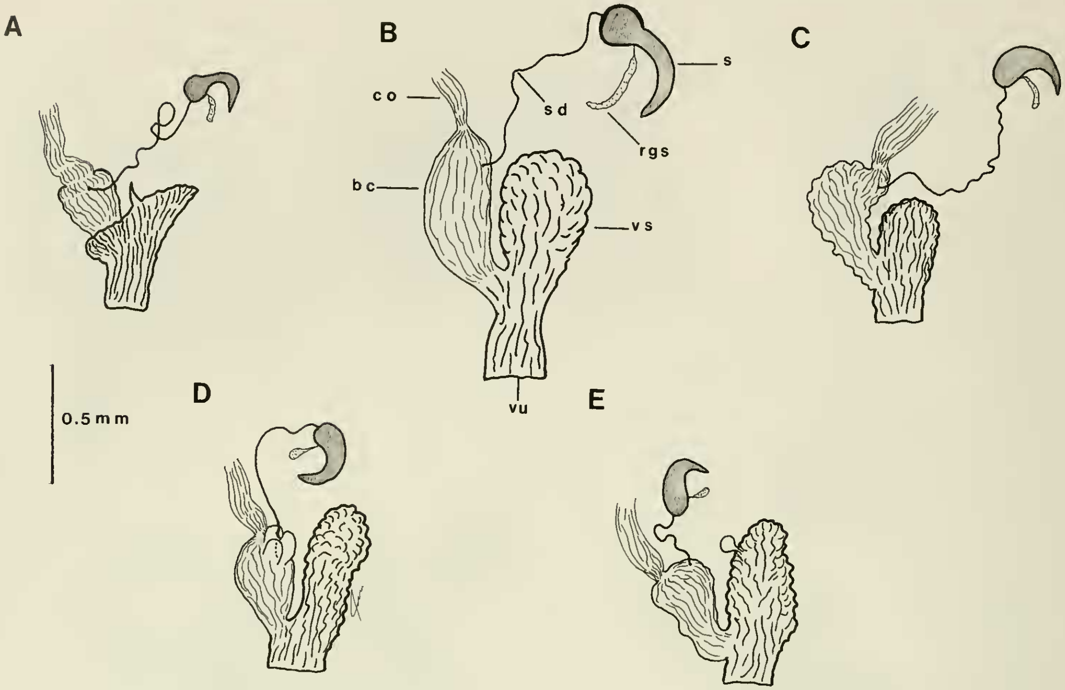

Fig. 5. Genital chambers in Eupariinae females after treatment with potassium hydroxide and chlorazol black. A, *Ataenius apicalis*. B, *At. sculptor*. C, *At. cribrithorax*. D, *At. setiger*. E, *At. paraperforatus*. (Abbreviations: bc = bursa copulatrix; co = common oviduct; rgs = reservoir of spermatheca gland; s = spermatheca; sd = spermathecal duct; vs = vaginal sac; vu = vulva or gonopore).

continue into the common oviduct, which in turn joins the genital chamber. Basal oocytes mature simultaneously in all ovarioles.

The genital chamber is bulky and surrounded by strong, numerous muscles (Fig. 4A). After treatment with potassium hydroxide, the bursa copulatrix is clearly seen dorsal to the vaginal sac (Fig. 5A). The bursa copulatrix is short and enlarged in its anterior region where the common oviduct joins it; subsequently it narrows until it joins the dorsal face of the vaginal sac, much before the vulva. The cuticular intima has thin walls and longitudinal folds. The spermathecal duct joins its medio-ventral anterior region, very close to the termination of the common oviduct.

The vaginal sac is fan shaped, with its anterior region much broader than its posterior region, from which it narrows until it terminates in the vulva. The cuticular intima is thicker here for the vaginal sac than for the bursa copulatrix, with a rough surface and longitudinal folds. In the mid-region of the broadest part, toward the ventral surface of the bursa copulatrix, there is a spine-like cuticular projection (Fig. 5A).

The spermatheca is wider and more sclerotized in the basal region, while its apical region is much thinner, pointed, and less sclerotized. From the basal region emerges a short spermathecal duct, which empties into the bursa copulatrix. The spermathecal gland reservoir is long and slender, and joins the medio-ventral anterior region of the spermatheca (Fig. 6A).

Comparison of *Ataenius* females.—The number of ovarioles per ovary differs from one *Ataenius* species to another, with 3 in *At. cribrithorax* and *At. setiger*, usually 8 in *At. apicalis*, 9 in *At. sculptor*, and 11 in *At. paraperforatus*. The number of ovarioles can also vary within any individual female of the same species. In *At. apicalis,* while there are generally 8 ovarioles in each ovary, there may be 7 or 8, or 8 and 9; and in *At. setiger,* which generally has 3 ovarioles per ovary, on rare occasions there may be 4 (Table 1).

The number of oocytes in the vitellarium varies according to species, with 2 in *At. apicalis,* 3 in *At. sculptor,* or 4 in *At. cribrithorax.* A mature basal oocyte measures 0.50 to 0.80 mm, depending on the species (Table 1). It seems that in all species oocyte maturation is simultaneous in all ovarioles of any female.

The bursa copulatrix leads into the dorsal surface of the vaginal sac in all species (Fig. 5). The anterior region of the cuticular intima is thin with few folds in *At. sculptor, At. cribrithorax,* and *At. parapeforatus* (Figs. 5B, C, D), while it is broader and shows more folds in *At. apicalis* and *At. setiger* (Figs. 5A, E). The vaginal sac is long, except in *At. apicalis,* in which is fan shaped. The cuticular intima of the vaginal sac is much thicker than that of the bursa copulatrix; the cuticular intima has a rough surface and numerous longitudinal folds. The folds are not so notable in *At. sculptor* (Fig. 5B), but very notable in *At. apicalis, At. cribrithorax, At. paraperforatus,* and *At. setiger* (Figs. 5A, C, D, E). A spine-like structure is found on the dorsal surface of the vaginal sac only for *At. apicalis,* while a spherical structure similarly is found in *At. paraperforatus* (Figs. 5A, D).

The spermatheca is relatively wide at its base and its apex is relatively pointed in all species studied. The base is more rounded and sclerotized in *At. sculptor* (Fig. 6B). The spermathecal duct is short in all species, measuring about 1 mm, and begins at the base of the spermatheca. On dissection, the spermathecal gland is large, with a rough surface (Fig. 4). The cuticular reservoir of the spermathecal gland is long in all species, although its size varies from one species to another (Fig. 6). The spermathecal gland duct terminates in the medio-ventral anterior region of the spermatheca in all species (Fig. 6).

Comparison of *Aphodius, Cephalocyclus,* and *Ataenius* females.—*Aphodius, Cephalocyclus,* and *Ataenius* females all show the same general scheme of reproductive system, though some differences are found. The number of ovarioles varies among species in the same genus, from one subfamily to another, and in some cases intraspecifically as well (Table 1). These characteristics are also found in other species of Aphodiinae, Eupariinae, and Psamodiinae, insofar as the number of ovarioles is known (Table 2).

The common oviduct leads into the anterior section of the genital chamber in *Aphodius* and *Ataenius* species, while in *C. hogei* the common oviduct joins the vagina (Figs. 2, 5).

The genital chamber along with bursa copulatrix and vaginal sac are present in *Aphodius* and *Ataenius* species, but not in *Cephalocyclus,* in which only a sacular genital chamber or vagina is observed (Figs. 2, 5). The termination of the bursa copulatrix and of the vaginal sac are at about the same height in *Aphodius*; in *Ataenius,* the termination of the bursa copulatrix is in the dorsal wall of the vaginal sac. Most likely the vaginal sac serves to restrain the internal sac during copulation so that the ejaculatory duct penetrates as far as the anterior section of the bursa copulatrix at the same height as the spermathecal duct opening.

The spermathecal duct terminates close to the termination of the common oviduct in a highly folded structure in *Aphodius* and an unfolded structure in *Ataenius*; while in *C. hogei* the spermathecal duct simply terminates in the vaginal wall, relatively far from the end of the common oviduct (Figs. 2, 5).

The form of the spermathecal capsule differs among the various species of *Aphodius* and *Ataenius* and *C. hogei.* The spermathecal duct is very long in *Aphodius* species and *Cephalocyclus,* but relatively short in *Ataenius* species. The spermathecal

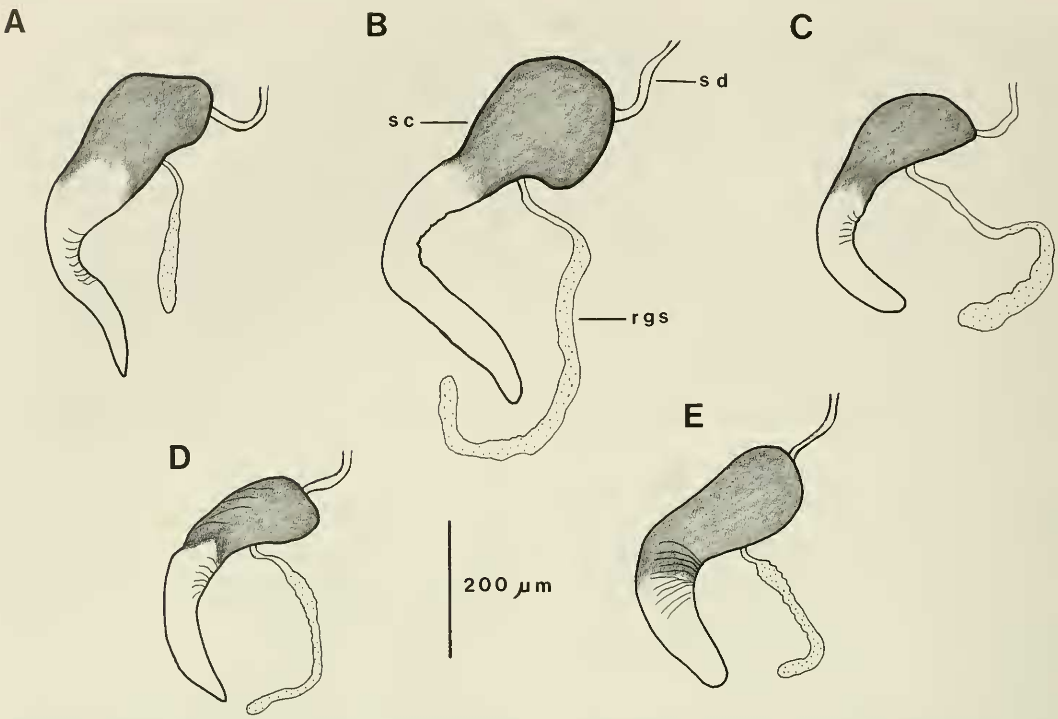

Fig. 6. Spermatheca schemes in Eupariinae females. A, *Ataenius apicalis.* B, *At. sculptor.* C, *At. cribrithorax.* D, *At. setiger.* E, *At. paraperforatus.* (Abbreviations: sd = spermathecal duct; rgs = reservoir of the spermatheca gland; sc = spermathecal capsule).

gland varies among species, as does the form of its reservoir and the placement of its opening in the spermatheca. The spermathecal gland terminates in the base of the spermatheca beside the opening of the spermathecal duct in *Aphodius,* while in *Ataenius* species and *Cephalocyclus* it terminates in the medio-ventral anterior region of the spermatheca (Figs. 2, 3, 5).

Males

The reproductive system in individual *Aphodius, Cephalocyclus,* and *Ataenius* males consists of 2 testes and 2 vasa deferentia, 2 accessory glands with their respective glandular reservoirs and glandular ducts, and an ejaculatory bulb that terminates in the aedeagus (Fig. 7).

Aphodius ophistius (Fig. 7A).—Each testis has 7 spherical follicles of the same size; the corresponding vas efferens is slender and short. The vas efferens terminate in their respective vas deferens. The vasa deferentia are curled up beneath the testis and continue until they terminate in the anterior region of the ejaculatory bulb.

Accessory glands appear as very long filaments. Each gland terminates in a fusiform glandular reservoir, from which the glandular duct emerges medio-ventrally. The glandular duct is narrow and terminates parallel to the vas deferens in the anterior region of the ejaculatory bulb.

The ejaculatory bulb itself is relatively large and complex, with a very thick, external muscular wall. This wall houses not only the ejaculatory duct itself but also the anterior section of the internal sac. The ejaculatory duct is found in the anterior region of the bulb where the vas deferens and glandular ducts terminate, has its own muscular wall, and folds back onto itself until it terminates in the anterior part of the internal sac. The anterior section of the inter-

Table 2. Number of ovarioles per ovary in females of Aphodiinae, Eupariinae, and Psammodiinae species, as reported in the literature.

Species	Ovarioles (number)*	Authors
APHODIINAE		
Aphodius (Aphodius) fimetarius	7–7	Stein 1847, Willimzik 1930, Gittings & Giller 1997
A. (Aphodius) elegans	7–7	Yoshida 1994
A. (Teuchestes) fossor	7–7	Willimzik 1930, Ritcher & Baker 1974, Gittings & Giller 1997
A. (Othophorus) haemorrhoidalis	5–5	Ritcher & Baker 1974, Yoshida 1994
A. (Othophorus) brachysomus	7–7	Yoshida 1994
A. (Colobopterus) quadratus	5–5	Yoshida 1994
A. (Colobopterus) erraticus	5–5	Gittings & Giller 1997
A. (Agrilinus) pratensis	5–5	Yoshida 1994
A. (Agrilinus) breviusculus	5–5	Yoshida 1994
A. (Agrilinus) sordidus	5–5	Yoshida 1994
A. (Agrilinus) ater	5–5	Gittings & Giller 1997
A. (Agrilinus) rufus	5–5	Gittings & Giller 1997
A. (Acrossus) depressus	11–11	Gittings & Giller 1997
A. (Acrossus) rufipes	7–7	Gittings & Giller 1997
A. (Melinopterus) prodromus	5–5	Gittings & Giller 1997
A. (Melinopterus) sphacelatus	4/5–4/5*	Gittings & Giller 1997
A. (Chilothorax) inquinatus (=*distinctus* Muller)	5–5	Willimzik 1930
A. (Chilotorax) distinctus	5–5	Ritcher & Baker 1974
A. (Pseudogolius) coloradensis	5–5*	Ritcher & Baker 1974
A. (Tetraclipeodes) denticulatus	5–5	Ritcher & Baker 1974
A. (Calamosternus) granarius	5–5	Ritcher & Baker 1974; Gittings & Giller 1997
A. (Labarrus) lividus	5–5	Ritcher & Baker 1974
A. (Koshantschikovius) fucosus	6–6	Ritcher & Baker 1974
A. (Cinacanthus) hirsutus	6–6*	Ritcher & Baker 1974
A. (Esymus) pusillus	5–5	Yoshida 1994
A. (Phaeaphodius) rectus	7–7	Yoshida 1994
Xeropsammobeus desertus	5–5	Ritcher & Baker 1974
Aegialia blanchardi	3–3	Ritcher & Baker 1974
EUPARIINAE		
Ataenius cognatus	3–3	Ritcher & Baker 1974
At. deserta	3–3	Ritcher & Baker 1974
PSAMMODIINAE		
Psammodius oregonensis	3–3*	Ritcher & Baker 1974
Trichiorhyssemus riparius	2–2	Ritcher & Baker 1974
Pleurophorus caesus	2–2	Ritcher & Baker 1974

* Number of ovarioles per ovary can vary in females of the same species.

nal sac occupies the posterior half of the ejaculatory bulb; on dissection, it can clearly be seen, given its highly ornamented cuticular form. The posterior part of the ejaculatory bulb is found within the aedeagus. The ventral preputial gland is found at the same level as the aedeagus parameres bases.

After treating the ejaculatory bulb with potassium hydroxide and staining it with chlorazol black, the ejaculatory duct's cuticular intima and the internal sac can be clearly seen. The ejaculatory duct is long—when extended it measures longer than the total length of the ejaculatory bulb—and is divided into two regions. The anterior part,

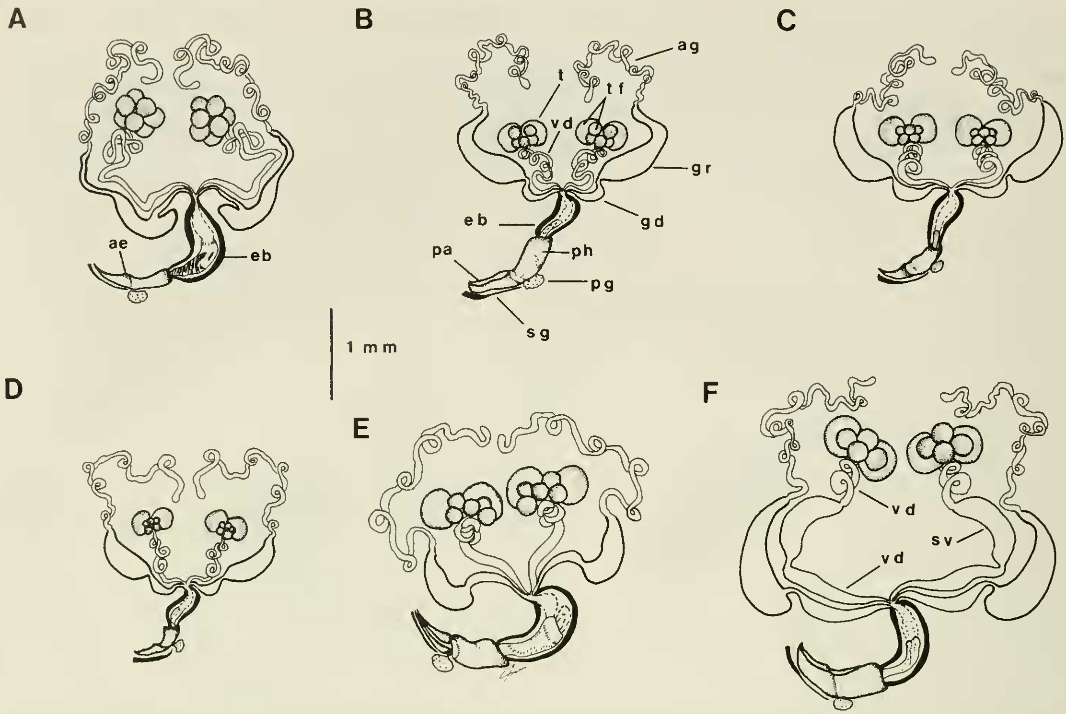

Fig. 7. Schematic of reproductive system in Aphodiinae males. A, *Aphodius opisthius.* B, *A. sallei.* C, *A. vittatus.* D, *A. nigrita.* E, *A. pseudolividus.* F, *Cephalocyclus hogei.* (Abbreviations: ae = aedeagus; ag = accessory glands; eb = ejaculatory bulb, including the ejaculatory duct and the anterior part of the internal sac; gd = glandular duct; gr = glandular reservoir; pg = ventral preputial gland; pa = paramere; ph = phallobase; sg = spiculum gastrale; t = testis; tf = testicular follicles; sv = seminal vesicle; vd = vas deferens).

in which the vasa deferenentia and glandular ducts terminate, is wide, taking the form of a funnel with low-cut borders, having a smooth, sclerotized cuticular intima. The posterior part, which terminates in the internal sac is long and narrow; its cuticular intima is smooth, slightly folded, and less sclerotized. The anterior part of the internal sac, which is found within the ejaculatory bulb, is wide, very sclerotized, and very ornamented; its posterior part, which is found in the aedeagus, is narrow, sclerotized, and ornamented (Figs. 8A, 9A).

Comparison of *Aphodius* males.—*Aphodius pseudolividus* males have been described in detail by Pluot-Sigwalt and Martínez (1998); therefore we omit related histological details, considering that few differences are found at this level. In fact, *A. pseudolividus* has been included in this study largely as a point of comparison. We found that this species shares some characters the reproductive system with the other species examined, but it presents differences as well.

Aphodius species have 7 testicular follicles. In most, the testicular follicles are of different sizes within an individual of any species: *A. vittatus, A. sallei, A. nigrita,* and *A. pseudolividus* all have 2 large follicles and 5 small ones; an exception to this rule is *A. opisthius,* which has testicular follicles of the same size.

Accessory glands are long filaments in all species examined. A saculiform glandular reservoir is found in all species. The glandular duct begins in the posterior part of the glandular reservoir in most species, except in *A. opisthius,* in which it begins in the medio-ventral region (Fig. 7).

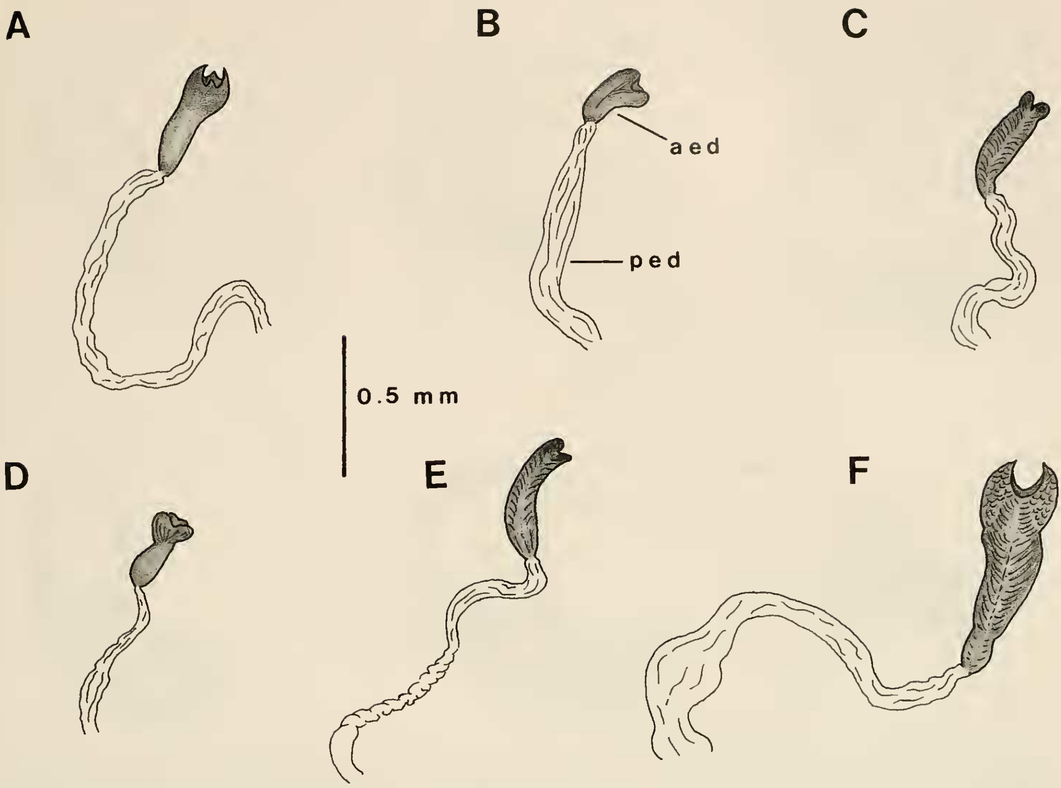

Fig. 8. Schematics of ejaculatory ducts in Aphodiinae males. A, *Aphodius opisthius*. B, *A. sallei*. C, *A. vittatus*. D, *A. nigrita*. E, *A. pseudolividus*. F, *Cephalocyclus hogei*. (Abbreviations: aed = anterior section of the ejaculatory duct, where the vas deferens and glandular ducts terminate; ped = posterior section of the ejaculatory duct, which terminates in the anterior part of the internal sac).

The ejaculatory bulb is found in all species, but the ejaculatory duct and internal sac differ from one species to another. The ejaculatory duct is longer than the ejaculatory bulb in all species studied, though it is very long in *A. opisthius* and *A. pseudolividus,* and relatively short in *A. sallei, A. vittatus,* and *A. nigrita* (Figs. 8, 9). The form of borders in the anterior part of the ejaculatory duct differs among species, while the cuticular intima may be smooth and without spines, as in *A. opisthius, A. sallei,* and *A. nigrita* (Figs. 8A, B, D), or have spines, as in *A. vittatus* and *A. pseudolividus* (Figs. 8C, E). The anterior region of the internal sac, which is observed internally in the posterior area of the ejaculatory duct, is highly cuticular and presents ornamentation that differs from one species to another (Fig. 9). All *Aphodius* species have a ventral preputial gland (Fig. 7).

Cephalocyclus hogei (Fig. 7F).—Each testis has 6 follicles of different sizes, with 2 of the follicles being larger than the other 4. The vas deferens show three different regions: (1) The anterior part, which is short, thick, and rolled up beneath the testicle; (2) the intermediate part, which is a saculiform vesicle that narrows at its base, and which continues, forming; and (3) the posterior region of the vas deferens, which runs into the ejaculatory duct. Most likely, the intermediate region functions as a seminal vesicle.

The accessory glands form long filaments, running into the saculiform glandular reservoir, which in turn terminates in the last third of the glandular duct ventrally.

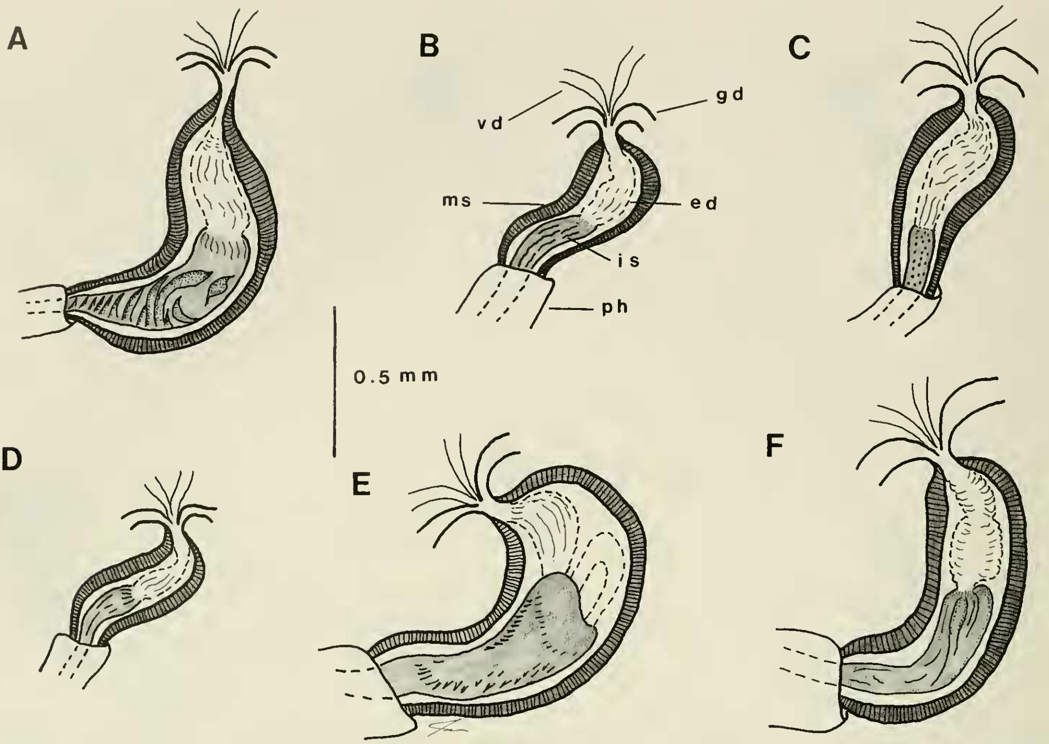

Fig. 9. Diagrams of ejaculatory bulbs in Aphodiinae males. A, *Aphodius opisthius.* B, *A. sallei.* C, *A. vittatus.* D, *A. nigrita.* E, *A. pseudolividus.* F, *Cephalocyclus hogei.* (Abbreviations: ed = ejaculatory duct; gd = glandular duct; is = internal sac [anterior section]; ph = phallobase; vd = vas deferens; ms = muscular sheath).

The glandular ducts terminate parallel to the vas deferens, in the anterior section of the ejaculatory bulb.

The ejaculatory bulb is similar in many ways to that seen in *Aphodius* species. After treatment with potassium hydroxide and staining, the ejaculatory duct, when extended, is seen to be longer than the ejaculatory bulb. The anterior section of the ejaculatory duct, where the vasa deferentia and glandular ducts terminate, is wide, with low-cut borders bearing ornamentation and spines, and a highly sclerotized cuticular intima. The posterior region is much narrower, less sclerotized, and folded until it reaches the anterior part of the internal sac (Fig. 8F). The internal sac is strongly sclerotized, presenting long ornamentations (Fig. 9F). A ventral preputial gland is present (Fig. 7F).

Ataenius apicalis (Fig. 10A).—Each testis is formed of two oval follicles with their respective vas efferens. The two vasa efferentia terminate in the corresponding vas deferens. The vasa deferentia have a thin wall, with the slendor anterior section folded back on itself, after which these organs thin further as they continue to an unfolded posterior region of much greater diameter, but which thins considerably as it terminates in the ejaculatory bulb.

The accessory glands are long filaments, continuing with the glandular reservoir, which itself has two regions: (1) The long anterior region, of greater diameter than the glands; and (2) the posterior region which doubles back to form a blocked sac. At the base of the sac is a short, narrow duct that terminates in the anterior region of the glandular duct, which in turn narrows and then terminates in the anterior part of the ejaculatory bulb. Glandular secretions can be found in the anterior part of the reservoir,

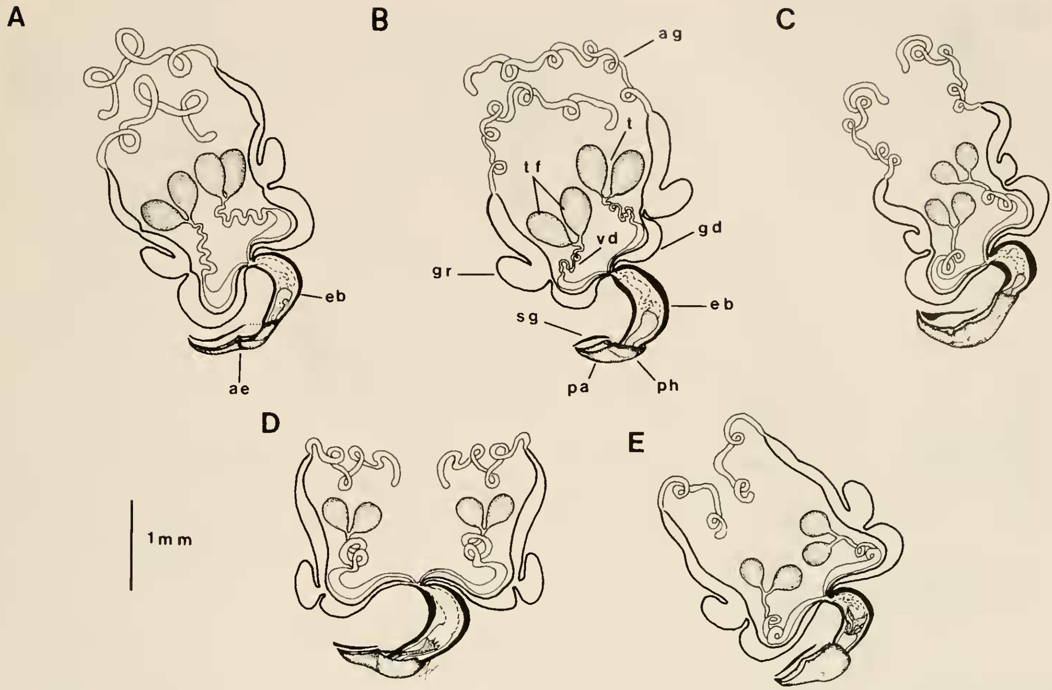

Fig. 10. Schematics of Eupariinae male reproductive system. A, *Ataenius apicalis*. B, *At. sculptor*. C, *At. cribrithorax*. D, *At. setiger*. E, *At. paraperforatus*. (Abbreviations: ae = aedeagus; ag = accessory glands; eb = ejaculatory bulb, including the ejaculatory duct and internal sac; gd = glandular duct; gr = glandular reservoir; pa = paramere; ph = phallobase; sg = spiculum gastrale; t = testis; tf = testicular follicles; vd = vas deferens).

which apparently functions as a duct secretion collector, and in the anterior part of the glandular duct, but they are mainly accumulated in the blind sac that functions as a true reservoir.

The ejaculatory bulb has a thick muscular wall. The two vasa deferentia and two glandular ducts terminate in the bulb's anterior part, and the base of the aedeagus terminates in its posterior part. In its interior, the ejaculatory duct and anterior section of the internal sac are found. The ejaculatory duct has its own muscular wall, and it terminates in the anterior section of the internal sac, which is highly sclerotized and ornamented.

After treatment with potassium hydroxide, the ejaculatory bulb can be clearly observed. It is a relatively short and folded duct, which ends by joining the internal sac. It consists of two parts: the anterior section, in which the vasa deferentia and glandular ducts terminate, is funnel-shaped, with a thick and spiny cuticular intima; and the posterior section, which terminates in the internal sac, consists of a narrower duct with a thin and very slighly folded cuticular intima (Fig. 11A). The internal sac is highly sclerotized and ornamented (Figs. 11A, 12A).

Comparison of *Ataenius* males.—The same general scheme of reproductive system is present in all species examined. All species have two follicles per testicle, though their size varies with species (Table 3). Accessory glands, with their reservoirs and ducts, show the same general pattern anatomically. Ejaculatory ducts vary from species to species, above all the morphology of the anterior section, though in all species examined the cuticular intima in this region presented cuticular spines (Figs. 11A, B, C, D). The internal sac differs among species also, including its ornamen-

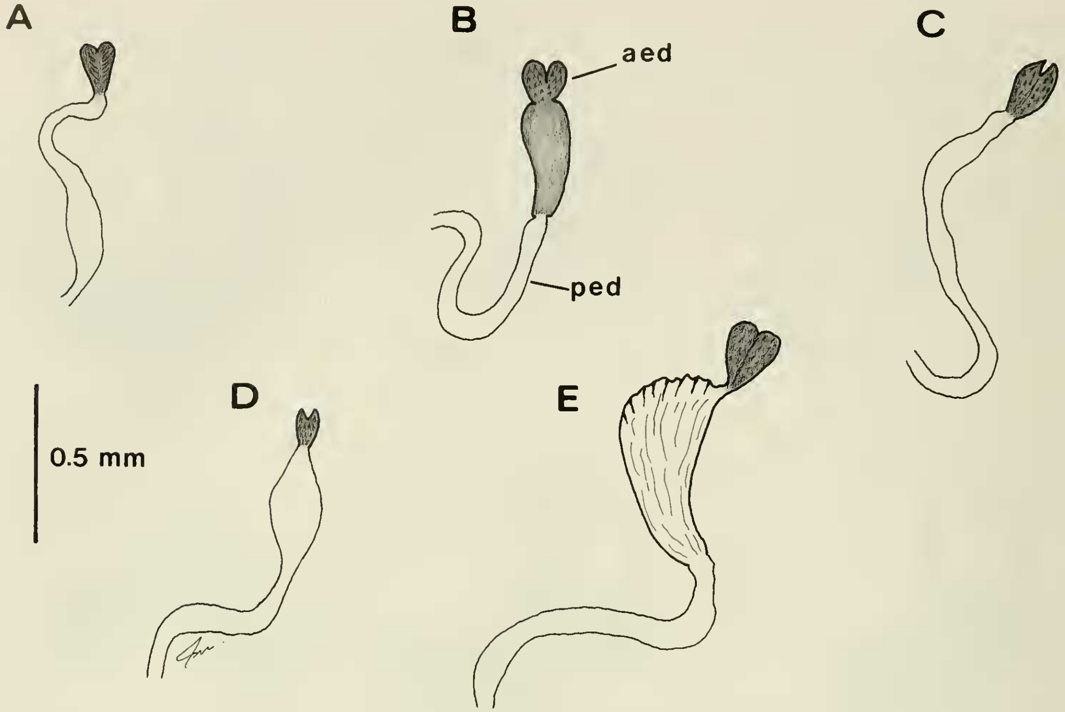

Fig. 11. Diagrams of Eupariinae male ejaculatory ducts: A, *Ataenius apicalis.* B, *At. sculptor.* C, *At. cribrithorax.* D, *At. setiger.* E, *At. paraperforatus.* (Abbreviations: aed = anterior region of the ejaculatory duct, where the vas deferens and glandular ducts terminate; ped = posterior part of the ejaculatory duct which terminates in the anterior region of the internal sac).

Table 3. Anatomical data on the male reproductive system in Aphodiinae and Eupariinae (n, number of the individual males examined per species in the present study).

Species	Individuals (n)	Testis Follicles: Total Number	Testis Follicles: (Number) of a Given Size (mm)	Preputial Glands Presence (X)
APHODIINAE				
Aphodius opisthius	30	7	(7) 0.26	X
A. vittatus	20	7	(2) 0.38 + (5) 0.15	X
A. sallei	20	7	(2) 0.32 + (5) 0.16	X
A. nigrita	6	7	(2) 0.26 + (5) 0.13	X
A. pseudolividus	25	7	(2) 0.44 + (5) 0.22	X
Cephalocyclus hogei	30	6	(2) 0.38 + (4) 0.26	X
EUPARIINAE				
Ataenius apicalis	30	2	(2) 0.60	—
At. sculptor	30	2	(2) 0.96	—
At. cribrithorax	20	2	(2) 0.40	—
At. setiger	10	2	(2) 0.45	—
At. paraperforatus	9	2	(2) 0.40	—

Table 4. Anatomical data on the male reproductive system in Aphodiinae and Eupariinae species as reported in the literature.

Species	Follicles per Testis: Of Same Size	Follicles per Testis: Of Different Size	Preputial Gland Presence (X)	Authors
APHODIINAE				
Aphodius (Aphodius) fimetarius	6	—	—	Bordas 1900
	—	5 + 2	X	Pluot-Sigwalt & Martínez 1998
A. (Aphodius) coniugatus	7	—	—	Bordas 1900
A. (Phalacronotus) quadrimaculatus	6	—	—	Bordas 1900
A. (Nialus) varians	6	—	—	Bordas 1900
A. (Agrilinus) ater	—	5 + 2	X	Pluot-Sigwalt & Martínez 1998
A. (Biralus) satellitius	—	5 + 2	X	Pluot-Sigwalt & Martínez 1998
A. (Bodilus) sallei	—	5 + 2	X	Pluot-Sigwalt & Martínez 1998
A. (Calamosternus) granarius	—	5 + 2	X	Pluot-Sigwalt & Martínez 1998
A. (Colobopterus) erraticus	—	5 + 2	X	Pluot-Sigwalt & Martínez 1998
A. (Coprimorphus) scrutator	—	5 + 2	X	Pluot-Sigwalt & Martínez 1998
A. (Labarrus) pseudolividus	—	5 + 2	X	Pluot-Sigwalt & Martínez 1998
*A. (Platyderides) fuliginosus**	—	5 + 2	X	Pluot-Sigwalt & Martínez 1998
A. (Teuchestes) fossor	6	—	—	Bordas 1900
	7	—	X	Pluot-Sigwalt & Martínez 1998
A. (Trichaphodius) opisthius	7	—	X	Pluot-Sigwalt & Martínez 1998
EUPARIINAE				
Ataenius cribrithorax	2	—	—	Pluot-Sigwalt & Martínez 1998
At. sculptor	2	—	—	Pluot-Sigwalt & Martínez 1998

* Recently this species was transferred to the genus *Cephalocyclus* (Dellacasa, M. et al., 1998).

tation patterns (Fig. 12). None of these species has a preputial gland.

Comparison of *Aphodius, Cephalocyclus,* and *Ataenius* males.—The number of testicular follicles per testis is 7 for *Aphodius,* 6 for *Cephalocyclus,* and 2 for *Ataenius,* consistent with other observations of *Aphodius* and *Ataenius* species (Tables 3 and 4). In *Aphodius fossor* and *A. opisthius,* the 7 follicles are of the same size, while in other *Aphodius* species 2 follicles are larger than the other 5, and in *Cephalocyclus* 2 follicles are larger than the other 4 (Tables 3 and 4).

The seminal vesicle is found only in *C. hogei*; none is found in *Aphodius* or *Ataenius* species (Figs. 7 and 10).

Accessory glands are longer in species of *Aphodius* and *Cephalocyclus* than in those of *Ataenius.* The glandular reservoir is straight in *Aphodius* and *Cephalocyclus,* but in *Ataenius* it has a blind sac in the posterior region. The glandular duct that emerges from the glandular reservoir begins in the posterior section in *Aphodius, Cephalocyclus,* and *Ataenius,* though in *A. opisthius* it emerges medio-ventrally (Figs. 7, 10).

The ejaculatory bulb has a thick muscular wall that contains the ejaculatory duct and also the anterior section of the internal sac in *Aphodius, Cephalocyclus,* and *Ataenius* species (Figs. 9, 12). The ejaculatory duct is longer in *Aphodius* and *Cephalocyclus* species than in *Ataenius,* but in all three genera the anterior section is relatively sclerotized, with ornamentation or spines. In *Aphodius, Cephalocyclus,* and *Ataenius,* the cuticular intima of the ejaculatory duct's anterior region has a morphology that is characteristic for any particular species, while the posterior region has a thin, smooth cuticular intima, on occasion with folds (Figs. 8, 11). The internal sac has a highly sclerotized and ornamented cuticular wall in all species studied, though the

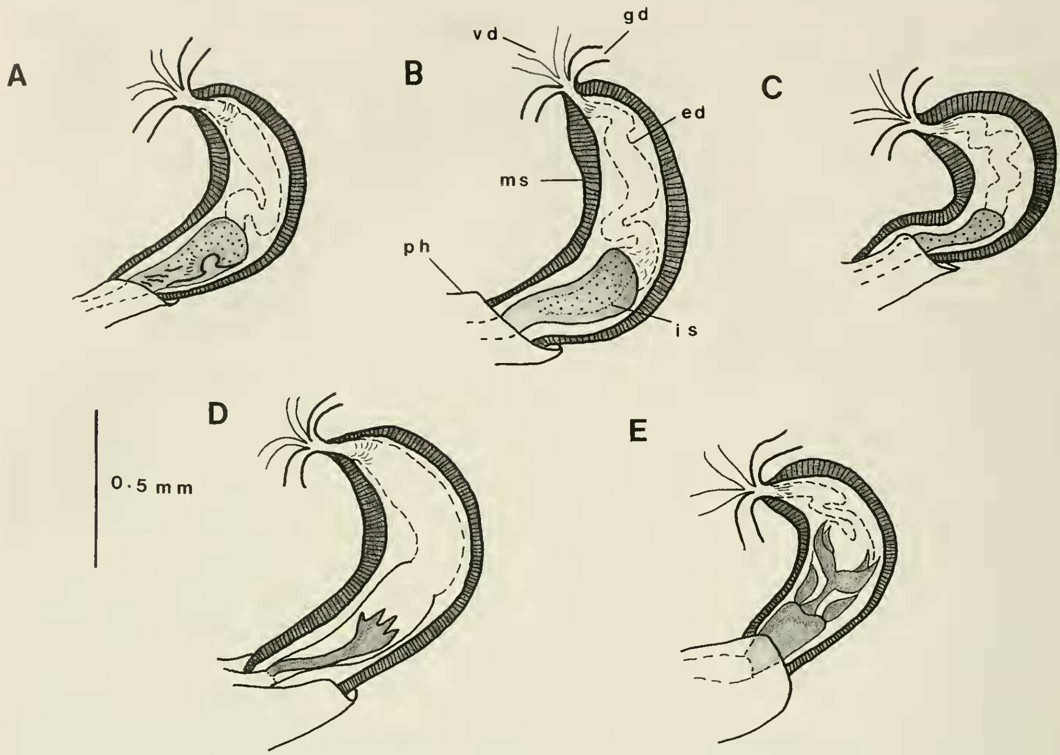

Fig 12. Schematics of ejaculatory bulbs in Eupariinae males. A, *Ataenius apicalis.* B, *At. sculptor.* C. *At. cribrithorax.* D, *At. setiger.* E, *At. paraperforatus.* (Abbreviations: ed = ejaculatory duct; gd = glandular duct; is = internal sac [anterior section]; ph = phallobase; vd = vas deferens; ms = muscular sheath).

specific type of ornamentions varies according to the species (Figs. 9, 12).

A ventral preputial gland is found in *Aphodius* and *Cephalocyclus,* but not in *Ataenius* (Figs. 7, 10).

Male insects form the spermatophore during copulation. The spermatophore consists principally of secretions of the accessory glands and vasa deferentia together with spermatozoa (Mann 1984). Until now, these features have not been examined for any Aphodiidae species. In the present study, observations of the genital chamber of females that recently copulated were immature, and without oocytes in *Ataenius apicalis, At. sculptor, At. cribrithorax,* and *At. paraperforatus,* and of some *Cephalocyclus hogei* females with small, maturing oocytes. No spermatophore was observed in any *Aphodius* species.

In *Ataenius* species and in *C. hogei,* the spermatophore is a large, whitish structure, which when recently formed completely distends the genital chamber, occupying a volume almost half as large as the female's abdominal cavity (Fig. 13).

Discussion

The reproductive system of females and males in the Aphodiinae and Eupariinae species examined are similar for each sex. However, there are differences among the species of the two subfamilies and between the two genera of Aphodiinae.

Females.—The number of ovarioles per ovary varies among *Aphodius, Cephalocyclus,* and *Ataenius* species, and they can vary among the females of the same species, just as in the other 33 species of these genera that have been studied (Table 2). However, is it not known whether the number of ovarioles is related to egg-laying be-

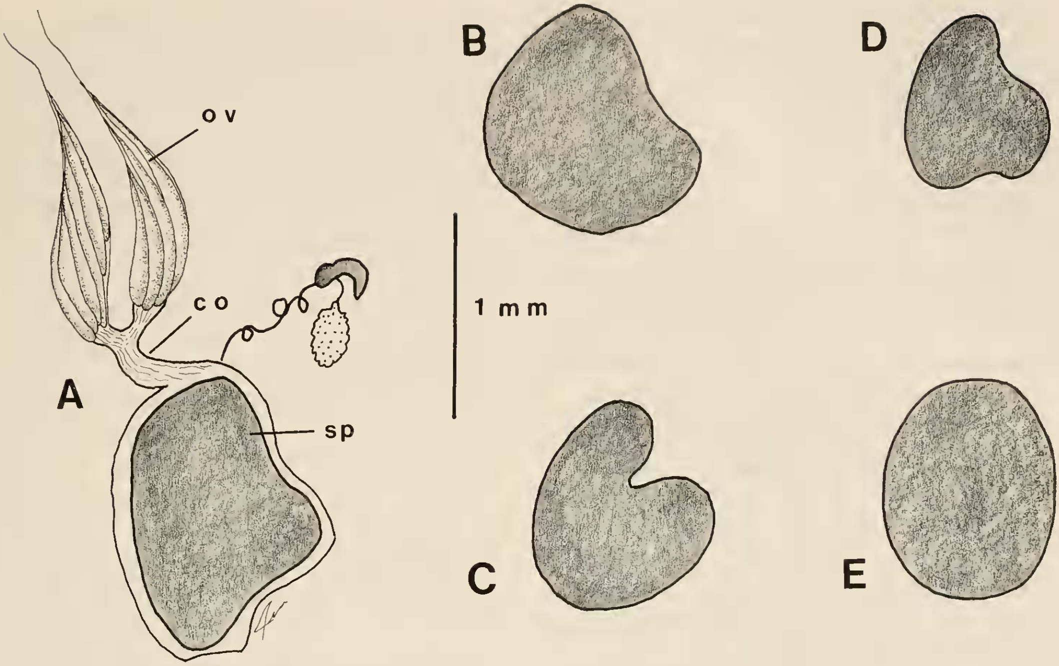

Fig. 13. Diagrams of spermatophores in A, *Ataenius apicalis*. B, *At. sculptor*. C, *At. cribrithorax*. D, *At. paraperforatus*. E, *C. hogei*. Only in the first species is the spermatophore shown in the genital chamber, though the spermatophore structure is found in all these species (Abbreviations: co = common oviduct; ov = ovary; sp = spermatophore).

havior or to the fecundity of the species for any Aphodiinae species.

Basal oocytes mature simultaneously in all *Aphodius, Cephalocyclus,* and *Ataenius* species studied. However until now, little has been known about whether one egg is laid, or several simultaneously, or about the fecundity (total number of eggs laid by the female of any particular species over her life span) of any of these species, data that are important in understanding reproductive cycles. Egg-laying behavior is known for only 20 *Aphodius* species. Some lay groups of eggs, the remainder single eggs. Depending on the species, the number of eggs laid at any one time varies from 1 to 18 (Willimzik 1930, White 1960, Rojewski 1983, Yoshida and Katakura 1992, Yoshida 1994, Palestrini and Barbero 1994, Gittings and Giller 1997). Fecundity is known for only 5 *Aphodius* species varying from 8 to 138 eggs laid per individual over a lifetime in females that have 5 or 7 ovarioles per ovary (Yasuda 1987, Yoshida 1994). Only Gittings and Giller (1997), based on the study of 10 *Aphodius* species of 8 subgenera, suggested a possible relationship between taxonomy and egg-laying behavior.

The bursa copulatrix and vaginal sac were here seen in *Aphodius* and *Ataenius* species, but not in *Cephalocyclus,* which simply has a sacular vagina. Willimzik (1930) described the vagina for *Aphodius fossor, A. fimetarius,* and *A. inquinatus* (= *A. distinctus* Muller), adding that in the two last species the dorsal region of the vagina is highly sclerotized and expanded; however, he did not indicate the separation between the bursa copulatrix and vaginal sac that surely exists in these species.

Males.—The number of testicular follicles found in *Aphodius* and *Ataenius* species is consistent with the observations of Pluot-Sigwalt and Martínez (1998) for other species in the same genera. *Aphodius* species always have 7 follicles in each testis.

Most of the species studied have testicular follicles of two sizes in any individual, while a minority have follicles of all one size. In contrast, *Cephalocyclus* has only 6 follicles of two different sizes per testis. Observations in other species and other genera show that differences may be found. Bordas (1900) noted that *A. fossor, A. fimetarius, A. quadrimaculatus,* and *A. varians* have only 6 testicular follicles, though these data need to be verified. Later observations in *A. fossor* and *A. fimetarius,* showed that all individuals of the species appear to have 7 follicles per testis (Pluot-Sigwalt and Martínez 1998).

In the present study, the seminal vesicle was observed only in *C. hogei*; this structure was not found in any species of *Aphodius* or *Ataenius.* In another comparative study of Scarabaeidae, Geotrupidae, and Aphodiidae males (Pluot-Sigwalt and Martínez 1998), the seminal vesicle was similarly not observed in any species. *Cephalocyclus hogei* males need to be studied to determine what is the significance of the seminal vesicle presence in the reproductive strategy of the species.

Accessory glands are commonly seen in males of the two subfamilies studied here, although they are longer in Aphodiinae than in Eupariinae species. Together the accessory gland secretions and the spermatozoa from the testis form the spermatophore during copulation. However, the spermatophore was observed only in several *Ataenius* species and *Cephalocyclus hogei*; apparently, *Aphodius* species do not form this structure.

Questions still remain about the nature of the spermatophore. Its formation might be related to the size of the spermatozoa. In *Aphodius, Cephalocyclus,* and *Ataenius* the spermatozoa are stored in the spermatheca (Imelda Marínez M., personal observations) to be used during fertilization of the oocytes, but the timing of copulation and the means by which the spermatozoa arrive at the spermatheca are not known. In the Aphodiinae species examined, the spermatozoa were large and of two sizes; these species also have two different sizes of testicular follicles. In *Aphodius,* the spermatozoa measure from 600 to 2,000 μm, depending on the size of the testicular follicle, while in *Ataenius* they measure from 120 to 160 μm (Martínez and Cruz 1999). In *C. hogei,* they are 800 to 1,500 μm (M. Cruz, unpublished observations).

In *Ataenius,* the size of the spermatozoa would not present an obstacle to the formation of the spermatophore, nor to the storage of the spermatheca. In contrast, in *Aphodius,* spermatozoa size could raise difficulties for both these processes, in particular, these species' spermatheca measures only between 200 and 300 μm. If in fact no spermatophore is formed in *Aphodius,* what function is played by the abundant secretions of the accessory glands? Research is needed on the role of secretions and the behavior of spermatozoa during and after copulation.

The ejaculatory bulb [in both the Aphodiinae and Eupariinae species] described in detail by Pluot-Sigwalt and Martínez (1998), is an organ with a strong muscular wall that contains the ejaculatory bulb proper and the anterior part of the internal sac. The bulb functions as a muscular pump to emit secretions and spermatozoa during copulation. The internal sac has a very sclerotized cuticular wall, which shows ornamentions in its anterior section that are characteristic of each species. Investigations are needed to ascertain whether the ornamentations have some relation to the morphology of the vaginal sac in females of the same species.

The preputial gland, seen only in Aphodiinae males, has been well described (Pluot-Sigwalt 1995, Pluot-Sigwalt and Martínez 1998). It apparently serves a lubricating function during copulation (Martínez and Linares 1994).

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